HISTORICAL PERSPECTIVE ESSAY

Phototropism: Bending towards Enlightenment

Research on phototropism has had far-reaching consequences in the field of plant biology, from helping to refute the ancient misconception of plant insensitivity to the environment to the discovery of the plant hormone auxin and the identification of the phototropin photoreceptors. In this essay, we trace the major trends and ideas that shaped past shoot phototropism research and briefly summarize the current state of the field.

ANCIENT AND MEDIEVAL PERCEPTIONS OF PHOTOTROPISM

For centuries, poets, philosophers, artists, and scientists have noted and studied the phototropic movement of plants. In one of the earliest depictions of plant phototropism, Venus, the ancient goddess of love, transforms Clytie, a water nymph, into a plant because of her infatuation with Apollo, the sun god. Associated with her metamorphosis into a green plant, Clytie turns and follows the movement of Apollo (Ovid et al., 1998). This tale of unrequited love is based on the assumption, developed by the early classical philosophers, that plants exhibit completely passive responses to the environment.

The earliest Greek philosophers, Anaxagoras (500–428 BCE) and Empedocles (495–435 BCE), believed that plants, like animals, are sensitive and capable of motion (Drossaart Lulofs and Poortman, 1989). Although Plato (427–347 BCE) also believed in plant sensitivity, he rejected the idea of plant movement (Shemp, 1947; Plato, 2000). Aristotle (384–322 BCE) argued that plants are totally passive and insensitive, and plant insensitivity served as a key criterion for distinguishing between plants and animals (McKeon, 1947; Drossaart Lulofs and Poortman, 1989). Following Aristotle's reasoning, Theophrastus (371–287 BCE) also considered plants as passive organisms. In his botanical writings, Theophrastus recorded the phototropic (and solar-tracking) tendencies of plants, but rather than implicating any activators in the plant, he attributed the phenomenon to the sun's activity in removing fluid from the illuminated side of the plant (Theophrastus, 1976). Because Aristotelian scientific philosophy placed greater value on logic alone and downplayed the need for experimental testing, Theophrastus' simple explanation of phototropism persisted until the 17th century when experimental botanists began to recognize plant sensitivity (Webster, 1966).

During the middle ages, herbalists were more interested in the medicinal properties of plants than understanding plant biology. According to the doctrine of signatures, which associated the shape of a plant with its medicinal usage, phototropic plants may have been prescribed for the treatment of snake and serpent bites due to the serpentine shapes they display (von Erhardt-Siebold, 1937). From today's scientific standpoint, the most significant advancement of the medieval herbals was the establishment of a nomenclature that separated plants whose flower-opening is dependent on the sun (composite) from plants that display shoot and leaf phototropism (solago) (von Erhardt-Siebold, 1937).

DISCOVERING THE INDUCTIVE NATURE OF PHOTOTROPISM

During the renaissance, some early scientists began studying "natural magic," which was reliant on the elements and occult properties of material things. In contrast with the Aristotelian disdain of experimentation, these early scientists used experimental observation in addition to classical texts to guide their thinking. Giambattista della Porta (1535–1615), probably one of the most well-known practitioners of natural magic, experimented with movement responses of cucumber seedlings. Drawing on Theophrastus' description of phototropism and anthropomorphic treatment of the response by medieval sources, della Porta described plant phototropism as a "rejoicing" response to the sun (della Porta, 1569). Furthermore, in an attempt to explain seemingly similar natural phenomenon, he proposed that the same fundamental law of nature, which he called "sympathy," governed the attraction of iron toward magnets, hens toward eggs, and the phototropic movement of plants toward the sun (della Porta, 1569). Although it is unclear if della Porta actually believed the concept of plant sensitivity, his explanation of phototropism as a rejoicing and sympathetic response helped open the debate on plant sensitivity.

Francis Bacon (1561–1626), who helped shape the modern scientific method, was familiar with della Porta's writing about plant movement. Bacon recorded the tropistic movements of many different plants but held to the classical belief in plant insensitivity. As such, Bacon discarded della Porta's explanation of plant phototropism as a sympathetic or rejoicing response to the sun, and, like Theophrastus, he viewed phototropism as a simple mechanical consequence of wilting. He wrote, "the cause (of phototropism) is somewhat obscure…the part beateth by the sun waxeth more faint and flaccid in the stalk, and less able to support the flower" (Bacon et al., 1627).

Intrigued by Bacon's discussion of plants, Thomas Browne (1605–1685) began studying plant physiology. As an alchemist, Browne was seeking a mystical unification of the universe and was more open to the idea of plant sensitivity than Bacon (Webster, 1966). At the time, plants were thought to emit "bad

air,'' so Browne believed that plant movements allowed plants to avoid the bad air produced by neighboring plants. In what is probably the first crude scientific experiment on plant phototropism, Brown observed that mustard seedlings grown in front of a basement window would eventually reorient themselves toward the window after he rotated the pot (Browne, 1658). When Robert Sharrock (1630–1684) repeated Browne's experiment, he concluded that the response was stimulated by fresh air and caused by growth rather than a mechanical consequence of wilting (Sharrock, 1672). These early phototropism experiments are significant because they provided some of the first scientific examples of plant sensitivity.

As the leading botanical taxonomist, John Ray (1628–1705) would have recognized the taxonomic implications that plant sensitivity would have on the classical distinction between plants and animals. To escape the problem this created, Ray considered phototropic movement of plants to be a mechanical effect of temperature on growth. Believing that the rapid etiolated growth of dark-grown seedlings was caused by warmer temperatures, Ray argued that phototropism is caused by a temperature gradient across the seedling with the side closest to the window being colder and slower-growing (Ray et al., 1686; Sachs et al., 1890). Although Ray's temperature hypothesis was later disregarded, his proposition that etiolated growth and phototropism are somehow connected remains a topic of investigation.

Due to the previous work of Browne and the discovery of the sensitive Mimosa plant, the idea of plant sensitivity to light began to receive wider acceptance (Webster, 1966). However, responsiveness to light was still considered to be mechanical rather than inductive. Although Charles Bonnet (1720–1793) attributed the process of photomorphogenesis to light, he failed to recognize the importance of light for phototropism. Instead, his phototropism experiments (Figure 1) led him to believe that plants were turning toward the warmth of the sun (Bonnet, 1754, 1779; Sachs et al., 1890). Yet based on Bonnet's observations, Henri-Louis DuHamel (1700–1782) concluded that light rather than warmth is more important for the response (DuHamel, 1758; Sachs et al., 1890).

The Romantic period of the late 18th and early 19th centuries was characterized by a philosophical backlash against the mechanistic view of life that had dominated the enlightenment, and the concept of an endogenous ''vital force'' served as a common explanation of plant phenomena (Sachs et al., 1890). As this outlook began losing popularity between 1820 and 1840, Henri Dutrochet (1776–1843) proposed that phototropism was an inductive response to light (Dutrochet, 1824, 1826, 1828, 1837). However, Dutrochet's contemporary, Augustin Pyramus de Candolle (1778–1841), thought that phototropism was simply a mechanical consequence of greater etiolated growth on the shaded side of the plant (de Candolle, 1832). This explanation of phototropism was challenged by Albert Bernard Frank (1839–1900), who was the first to propose that phototropism and gravitropism are inductive responses sharing a common under-
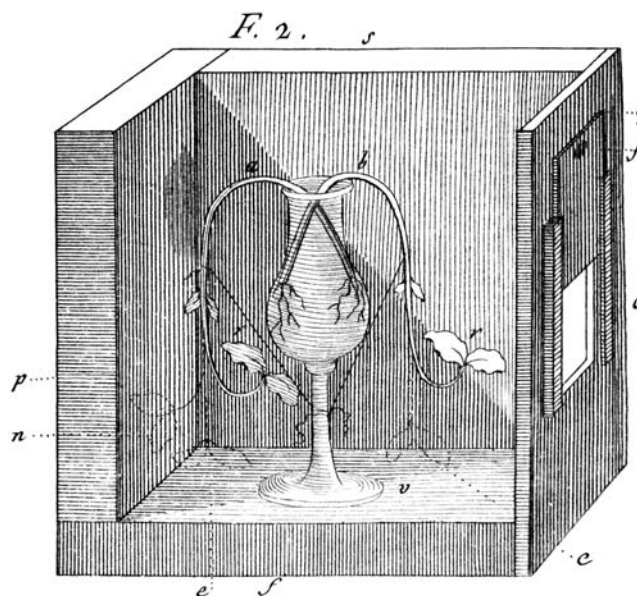
Figure 1. Woodcut Depicting a Charles Bonnet Tropism Experiment from 1779.

Two etiolated bean seedlings (*a* and *b*) oppositely placed in a vase (*v*) of water were tied downward (*e*). With the shutter (*f*) closed, each seedling reoriented upward toward the nearest wall (seedling *a* toward wall *q* and seedling *b* toward wall *p*). When the shutter was raised, both seedlings reoriented toward the opening (*o*). Reprinted from Bonnet (1779).

lying process (Frank, 1868). The inductive nature of the response was finally confirmed when Julius von Wiesner (1838–1919) showed that plants continue to bend toward a light source even after the light is turned off (von Wiesner, 1878).

Charles Darwin (1809–1882) further explored the inductive nature and mechanistic connection between phototropism and gravitropism. He proposed that the back and forth circumnutation associated with plant growth could be directed by a stimulus such as light or gravity (Darwin, 1880). Although Darwin's circumnutation theory of tropism served to propose a common mechanism underlying gravitropism and phototropism, the most significant discovery from his studies of plant movements was his demonstration that the site of photoperception at the shoot tip and the location of curvature are separable. From his observations, Darwin was able to propose that a transmissible substance produced in the tip is responsible for inducing curvature in lower regions of the plant (Darwin, 1880). This insightful discovery eventually lead to the discovery of the first plant hormone, auxin.

THE DISCOVERY OF AUXIN AND UNDERSTANDING ITS ROLE IN PHOTOTROPISM

Darwin's ideas were initially dismissed by other plant physiologists (reviewed in Heslop-Harrison, 1980). Nevertheless,

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evidence in favor of Darwin's transmissible substance began to accumulate when Rothert (1894) also showed that light sensitivity is greatest near the tip of maize coleoptiles. Subsequent results of Fitting (1907), Boysen-Jensen (1911), and Paal (1918) provided more direct evidence that a transmissible substance produced in the tip participates in the response. This research culminated in a model put forth independently by Cholodny (1927) and Went (1926, 1928), which proposed that light-mediated lateral redistribution of a plant growth hormone to the shaded side of the seedling causes the differential growth associated with phototropic curvature. This growth substance was shortly identified from human urine by Kogl and Haagen-Smit (1931), who named the hormone auxin, derived from the Greek verb auxein, meaning "to grow."

Although the Cholodny-Went model has remained the dominant explanation of phototropism, other models have challenged its validity. Historically, the model advocated by A.H. Blaauw has been one of the most common alternatives to the Cholodony-Went theory. Similar to Candolle, Blaauw proposed that phototropism is a secondary consequence of differential growth inhibition associated with photomorphogenesis (Blaauw, 1919). While arguing against the Blaauw theory as the sole basis for phototropism, Boysen-Jensen et al. (1936) and Went and Thimann (1937) held out the possibility that both models might function during the phototropic response of dicotyledonous plants. Evidence for this complementary Blaauw/Cholodony-Went model was based on the work of Overbeek, who demonstrated that although unilateral light stimulates the movement of auxin to the shaded side of the hypocotyl, up to half the differential growth associated with phototropism can be attributed to light-mediated growth inhibition (Overbeek, 1932, 1933). More detailed measurements of growth during the 1980s supported this view by indicating that growth inhibition on the illuminated side is accompanied by growth promotion on the shaded side of seedlings (Iino and Briggs, 1984; Macleod et al., 1985; Rich et al., 1985; Baskin, 1986). However, Cosgrove (1985) demonstrated that light-mediated growth inhibition occurs much sooner than the onset of phototropic curvature, a finding that would not be predicted by the Blaauw model. Additional evidence against the Blaauw model came from a study by Liscum et al. (1992), which demonstrated that growth inhibition and phototropism are separable.

Another major challenge to the Cholodny-Went model came from an experiment indicating that carotenoids (proposed phototropism photoreceptors) participate in photoinactivation of auxin (Kogl and Schuringa, 1944). This observation led to the hypothesis that phototropism is caused by differential carotenoid-mediated auxin inactivation (reviewed in Shank, 1950). Evidence against the auxin inactivation model came when Briggs et al. (1957) failed to see any in vivo change in total auxin concentration following treatment with light. Instead, their results showed that a barrier inserted between the illuminated and dark sides of the coleoptile prevents the development of an auxin gradient under unilateral illumination. Further support of the Cholodony-

Went model came when Briggs (1963a) reported a correlation between an auxin gradient and the magnitude of phototropic response and when Pickard and Thimann (1964) showed that unilateral blue light causes greater radiolabeled auxin accumulation on the shaded flank of coleoptiles. Although these key studies demonstrated that a differential auxin gradient is associated with phototropism, they could not resolve how this gradient develops.

According to the classical Cholodny-Went model, lateral auxin transport gives rise to phototropism. However, experiments by Shen-Miller and Gordon (Shen-Miller and Gordon, 1966; Shen-Miller et al., 1969) indicated that light inhibits polar auxin transport, which led them to propose that phototropism is caused by light-mediated inhibition of polar auxin transport on the illuminated flank of a seedling. Related to this model, Naqvi (1972) proposed that light-induced production of abscisic acid on the illuminated flank of the seedling causes unequal polar auxin transport. To test the idea that unequal polar auxin transport gives rise to phototropism, Gardner et al. (1974) followed radiolabeled auxin that had been asymmetrically applied to coleoptiles. Although they were not able to completely exclude a role for light-mediated inhibition of polar auxin transport, their results further demonstrated that unilateral blue light induced lateral auxin transport. At the same time, Kang and Burg (1974) reported that the enhancement of pea epicotyl phototropism by red light or gibberellins did not correlate with an increase in lateral auxin transport and proposed that the magnitude of the phototropic response is determined by adjusting auxin sensitivity. Altogether, these studies supported the involvement of auxin in phototropism, but the precise mechanism of how auxin transport and signaling cause phototropism remained unknown.

Many more details about how changes in auxin transport influence phototropism are now emerging from research using *Arabidopsis* as a model system. One report claims that mutations in *PIN3*, which encodes an auxin efflux carrier involved in lateral auxin transport, can disrupt phototropism (Friml et al., 2002). However the relationship between blue light signaling and PIN3 is uncertain. Work by Blakeslee et al. (2004) suggests that blue light does not effect the localization of PIN3 as it does for PIN1, an auxin efflux carrier thought to be important for polar auxin transport. Light-mediated relocalization of PIN1 appears to play a role in phototropism, as mutants in *MDR1*, a gene encoding a P-glycoprotein ABC transporter, show less PIN1 localization to the basal end of hypocotyl cells and an enhanced phototropic response (Noh et al., 2003). With less PIN1 localized to the basal end of hypocotyl cells, it was proposed that by decreasing polar auxin transport, phototropism may be enhanced by increasing the amount of auxin available for lateral transport (Noh et al., 2003). However, some polar auxin transport appears to be important for the normal progression of phototropism as *big* mutants, which have diminished polar auxin transport, display longer phototropic latent periods (Whippo and Hangarter, 2005). Clearly, more research is needed to determine how changes in

both lateral and polar auxin transport impact phototropism. In particular, it will be important to understand how the dynamics of auxin transport are regulated in the context of the differential growth responses that lead to curvature.

Although our knowledge about auxin transport has advanced significantly, we have an even better understanding of auxin signaling during phototropism and a compelling model is developing. An important study by Harper et al. (2000) showed that the *nonphototropic hypocotyl4* (*nph4*) locus encodes Auxin Response Factor7 (ARF7), a member of the auxin response factor family. ARFs function as transcriptional regulators whose activity is inhibited by binding to AUX/IAA proteins. Auxin facilitates ARF activity by promoting the targeting of AUX/IAA proteins for degradation via the ubiquitin-proteosome pathway (Liscum and Reed, 2002). With respect to phototropism, the degradation of IAA19, which binds to and inactivates ARF7, participates in phototropism under low light conditions (Tatematsu et al., 2004). However, ARF7 involvement in phototropism does not seem absolutely necessary, since *nph4/arf7* mutants display a phototropic response when treated with ethylene or given a red light pretreatment (Stowe-Evans et al., 2001). This suggests that red light or ethylene activates another ARF that functions during phototropism (Harper et al., 2000). A possible scenario is that the ARFs promote phototropism by controlling the expression of genes containing auxin response elements (AuxREs) (Liscum and Reed, 2002). In support of this scenario, a recent study found that eight genes with differential transcript accumulation across phototropic-stimulated *Brassica oleracea* hypocotyls have one or more AuxREs (Esmon et al., 2005). Interestingly, two of these genes encode expansins, which are involved in cell wall extension (Esmon et al., 2005). Therefore, this study provides a plausible mechanism linking the differential growth underlying phototropism to the auxin regulation of expansin activity (Esmon et al., 2005). Since the genes

encoding for AUX/IAA proteins also contain this AuxRE, a negative feedback loop involving the upregulation of AUX/IAA proteins may participate in the progression of normal phototropism (Tatematsu et al., 2004). For example, the reversal in the differential growth gradient that prevents the hypocotyl from curling around upon itself as the position of curvature migrates down the length of the hypocotyl (Silk, 1984; Whippo and Hangarter, 2003) may be a partial consequence of ARF-mediated upregulation of AUX/IAA proteins.

THE SEARCH FOR A PHOTOTROPISM PHOTORECEPTOR

In parallel with research on the role of auxin in phototropism, another important area concerns how plants perceive a unilateral light source. As soon as it became more widely accepted that phototropism is stimulated by light in the 1800s, the focus turned toward identifying the property of light responsible. As early as 1817, Sebastiano Poggioli reported that blue wavelengths of light are more effective at orienting plant growth (Poggioli, 1817). After several conflicting studies by Payer (1842), Zantedeschi (1843), Guillemin (1858), and Sachs (1864), Julius von Wiesner published the first methodical examination of the phototropism action spectra at specific wavelengths of light (Figure 2) and confirmed that phototropism is strongest toward blue/violet light (von Wiesner, 1878). Blaauw (1909) later identified a peak wavelength around 450 nm. Johnston elaborated on Blaauw's action spectra and identified dual peaks at 480 and 440 nm (Johnston, 1934).

When the action spectra for phototropism became better defined, attention turned toward identification of the blue light photoreceptor responsible for the response. Because the phototropism action spectra resemble the absorption spectra of carotenoids (Haig, 1935; Wald and Du Buy, 1936) and carotenoid concentration is greatest in the tips where phototropism
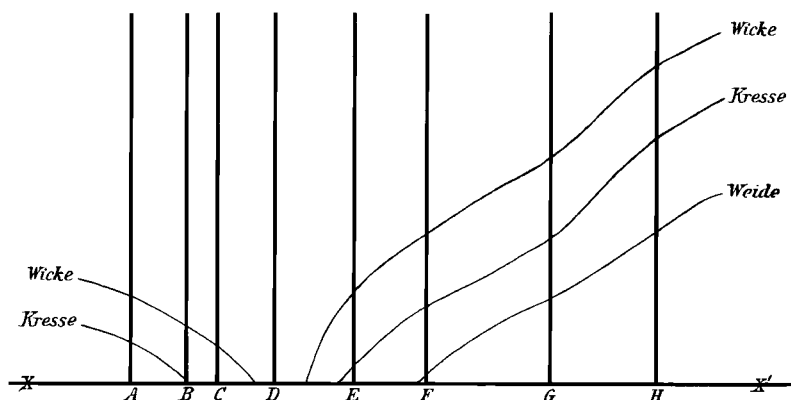
Figure 2. Julius von Wiesner's 1878 Diagram of the Action Spectra for Phototropism.

von Wiesner observed the phototropic response of pea (Wicke), cress (Kresse), and grass (Weide) seedlings to various light qualities. Letters along the *x* axis represent Fraunhofer lines demarking light quality between 759 nm (A) and 396 nm (H). Reprinted from von Wiesner (1878).

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sensitivity is greatest, carotenoids were originally considered to be the pigments responsible for phototropism (reviewed in Shank, 1950). This hypothesis went relatively unchallenged until Galston and Baker (1949) proposed the involvement of a flavin or flavoprotein photoreceptor during phototropism. The flavin hypothesis was primarily based on observations that flavins have a peak absorbance around 450 and that flavonoids can inactivate auxin in vitro (Galston, 1950).

For nearly the next 50 years, scientists would continue to debate the identity of the phototropism photoreceptor without convincing proof for or against either a flavonoid or carotenoid photoreceptor. One unfruitful line of research proposed that the blue light photoreceptor would be uncovered via studies of light-induced absorbance changes (Berns and Vaughn, 1970; Munoz and Bulter, 1975; Brain et al., 1977). Another line of research used chemical inhibitors to try to elucidate the identity of the blue light photoreceptor. Schmidt et al. (1977) and Vierstra and Poff (1981a) showed that maize coleoptiles treated with flavin inhibitors fail to display a phototropic response. However, carotenoids also appeared to play a role, perhaps as screening pigments, because coleoptiles treated with the carotenoid biosynthesis inhibitor norflurazon also show a reduced phototropic response (Vierstra and Poff, 1981b). In another study, Leong and Briggs (1982) hypothesized the involvement of a flavin cytochrome complex in the perception of light for phototropism because treatment with the electron transport chain inhibitor acriflourfen increased the sensitivity to unilateral blue light.

Eventually, Briggs and associates turned to a biochemical approach in an attempt to identify the blue light photoreceptor. Their work led to the identification of a 120-kD membrane-bound protein whose phosphorylation state and activation is altered by blue light in a fashion that correlated with phototropism (Gallanger et al., 1988; Short and Briggs, 1990; Reymond et al., 1992a; Short et al., 1992). Stronger evidence that this blue light phosporylated protein is involved in phototropism came when Reymond et al. (1992b) reported that microsomes from the phototropism mutant *JK224* contain lower levels of this 120-kD protein. The *JK224* mutant was originally isolated by Khurana and Poff (1989), who showed that it had a higher threshold requirement for the induction of phototropism and hypothesized that the mutant gene represented a photoreceptor involved in phototropism. Liscum and Briggs (1995) later identified other alleles of *JK224* in their screen for *nph* mutants, strengthening this hypothesis.

Cloning of *nph1* confirmed the prediction that this locus encodes the 120-kD protein (Huala et al., 1997), and subsequent biochemical evidence indicated that two domains of this protein, LOV1 and LOV2, bind to flavin chromophores with spectral properties consistent with phototropism (Huala et al., 1997; Christie et al., 1998, 1999). Hence, this protein was renamed phototropin (Christie et al., 1999), and the carotenoid-based photoreceptor hypothesis lost considerable ground. Still another photoreceptor was predicted to be involved in the induction of high-light phototropism because etiolated *phot1*

mutants retain a strong phototropic response to long-term irradiation with high-intensity blue light (Sakai et al., 2000). A subsequent study showed that another member of the phototropin family, phot2, functions redundantly to phot1 in the induction of high-light phototropism (Sakai et al., 2001).

With the identification of the phototropins as the phototropism photoreceptors, focus has turned to understanding their mechanism of light perception. Localization experiments reveled that more phot1 is located near the tip of etiolated seedlings than basally (Sakamoto and Briggs, 2002; Knieb et al., 2004), thus providing a possible reason for why Darwin observed greater sensitivity toward the tip (Darwin, 1880; Knieb et al., 2004). Salomon et al. (2000) presented evidence that light causes the formation of an adduct between a Cys residue located in the LOV domain and the flavin chromophore. In terms of the induction of phototropism and the light-mediated autophosphorylation of phot1, the LOV2 domain appears more critical than the LOV1 domain (Christie et al., 2002). However, how light-mediated autophosporylation leads to a phototropic response remains to be seen. One possibility is that a gradient of autophosphorylated phototropin across the seedling precedes the development of phototropic curvature (Salomon et al., 1997).

At this point, we know very little about the signaling components immediately downstream of the phototropins. NPH3 and RPT2, two related proteins with unknown function, bind to phot1 (Motchoulski and Liscum, 1999; Inada et al., 2004) and function very early in phototropin signaling. These proteins are clearly important for phototropism since of all the characterized phototropism mutants, only *nph3* mutants fail to show a response under any light condition (Liscum and Briggs, 1996; Sakai et al., 2000). While RPT2 is not necessary for phototropism, it participates in the promotion of high-light phototropism (Sakai et al., 2000). Future studies of NPH3, RPT2, and possibly other members of this family of proteins may become critical in uncovering how phototropin signaling modulates auxin transport. Calcium signaling has also been implicated as an early component of phototropin signaling (Gehring et al., 1990; Babourina et al., 2004). Although phot1 is required for a rapid blue light–mediated increase in cytosolic calcium (Baum et al., 1999) cytosolic calcium may not be necessary for phototropism (Folta et al., 2003). Instead, the phot1-induced increase in calcium seems to be more directly related to rapid phot1-mediated growth inhibition in hypocotyls (Folta et al., 2003).

PHYTOCHROME AND CRYPTOCHROME SIGNALING IN THE PROMOTION OF PHOTOTROPISM

The phototropins are not the only photoreceptors involved in phototropism. Although red light does not typically induce phototropism, a series of studies by Curry (1957), Blaauw-Jansen (1959), Asomaning and Galston (1961), and Briggs (1963b) showed that pretreating seedlings with red light modulates phototropic sensitivity to unilateral blue light. Implicating the phytochrome red/far-red reversible photoreceptors in phototropism,

Briggs (1963b) found that the red light enhancement of phototropism can be reversed by far-red light. This was later supported by a spectral correlation between phytochrome and the red light modification of phototropism (Chon and Briggs, 1966). Although these studies implicated a phytochrome role in phototropism, they could not address the relative importance of phytochrome activity in the promotion of phototropism.

Several studies indicated that phytochromes can play more than just a secondary role in phototropism under some circumstances. For example, Iino et al. (1984) proposed that phytochromes may be essential for phototropism in some cases because they observed a phototropic response of maize mesocotyls to unilateral red light. Since phytochromes also absorb blue light and saturating red or far-red light from above could inhibit the phototropic response of pea epicotyls, Parker et al. (1989) also concluded that pea epicotyl phototropism is primarily induced by phytochromes in conjunction with an unknown blue light photoreceptor, then referred to as cryptochrome, playing a secondary role. However, red light is generally much less effective at inducing phototropism (von Wiesner, 1878; Blaauw, 1909), so the phytochromes are not thought to be the directional photoreceptors in phototropism.

Several studies using *Arabidopsis* confirmed a significant role for the phytochromes, not only in the red light enhancement of phototropism (Parks et al., 1996; Hangarter, 1997; Janoudi et al., 1997a, 1997b; Stowe-Evans et al., 2001) but also in the absence of a red light pretreatment (Hangarter, 1997; Whippo and Hangarter, 2004). Likewise, other studies indicate that the cryptochrome blue light photoreceptors can enhance the development of phototropic curvature (Ahmad et al., 1998; Lasceve et al., 1999; Whippo and Hangarter, 2003). Since the phytochromes and cryptochromes function in parallel and somewhat redundantly during other light-mediated responses, they may be affecting phototropism in a similar fashion. Indeed, *phytochrome cryptochrome* double mutants display a severely reduced phototropic response under light conditions where *phytochrome* and *cryptochrome* single mutants show normal responses (C.W. Whippo and R.P. Hangarter, unpublished results). It is possible that the regulation of HY5, a transcriptional activator mainly associated with photomorphogenesis, by the phytochromes and cryptochromes participates in the promotion of phototropism because *hy5* mutants display a significantly slower phototropic response to very low light treatments (Whippo and Hangarter, 2005).

TOWARD UNDERSTANDING PHOTOTROPISM SENSITIVITY AND RESPONSIVENESS

The focus of phototropism research over the last 150 years was primarily concerned with the mechanistic aspects of the response. However, the degree to which a plant or plant part responds to unilateral light can vary widely. In some cases, different phototropic responses are a trivial result of mechanics: a large diameter shoot requires more differential growth than a small diameter shoot to reach the same angle of curvature. In other cases, differences in phototropism are more connected to the molecular physiology associated with changes in sensitivity and acclimation to prevailing light. Regulation of phototropism sensitivity/responsiveness can manifest itself in several different ways under long-term exposure to light or brief pulses of light.

The observation that etiolated seedlings exposed to continuous unilateral bright light have a slower response than seedlings exposed to continuous dim light was first observed by von Wiesner (1878). As already discussed, von Wiesner was investigating whether phototropism is a passive mechanical consequence of light or an inductive response. According to the hypothesis that phototropism is a passive mechanical phenomenon, brighter light was expected to cause a faster, stronger response. When testing this predication of the mechanical phototropism model, von Wiesner (1878) observed that increasing the light intensity past a certain threshold actually retarded the phototropic response of etiolated seedlings. However, von Wiesner also believed that the induction of phototropism was closely related to the induction of photomorphogenesis and concluded that the regulation of phototropic sensitivity and responsiveness coincides with light-mediated growth inhibition (von Wiesner, 1878). During the next century, Pringsheim (1912) and Ellis (1987) reconfirmed von Wiesner's initial observation, but a clear explanation of the phenomenon was not evident.

In a series of articles, Whippo and Hangarter (2003, 2004, 2005) studied the attenuating effect of continuous high light on the phototropic response of etiolated hypocotyls. From the results of these studies, it appears that there are at least two light-signaling pathways contributing to the attenuation of high-light phototropism. First, high light was found to cause a rapid phototropin-mediated decrease in phototropic responsiveness, as *phot1* mutants display a fairly rapid high-light response (Whippo and Hangarter, 2003). This may be due to high light–mediated desensitization of the phototropin photoreceptors or downstream effectors. Interestingly, RPT2 appears to partially mitigate the phot1-mediated attenuation of phototropism because RPT2 is not required for a high-light response in the absence of PHOT1 (Sakai et al., 2000). Secondly, after the rapid phot1-mediated attenuation, the cryptochromes and phytochrome A were found to help maintain a slower high-light phototropic response (Whippo and Hangarter, 2003, 2004). The cryptochromes and phytochrome A probably function somewhat redundantly in this process by regulating the photomorphogenic regulation of auxin signaling and transport (Whippo and Hangarter, 2005).

Although signaling elements associated with photomorphogenesis participate in the attenuation of high-light phototropism in etiolated seedlings, the relationship between development and phototropism is complex. In contrast with etiolated seedlings, Pringsheim (1912) observed that light-grown pea seedlings are more responsive to brighter light than to dimmer light. Similar behavior was observed in buckwheat (Ellis, 1987) and *Arabidopsis* (Whippo and Hangarter, 2005). However, how this

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developmental shift in phototropic sensitivity occurs is currently unknown.

Additional discoveries during the first decades of the 20th century also demonstrated that phototropic responsiveness to brief pulses of light is not as straightforward as might be expected. Using light pulses of varying duration or intensity, Blaauw (1909) determined that the magnitude of the response can be proportional to light dosage. Yet, Pringsheim (1909) and Clark (1913) soon reported that the reciprocity described by Blaauw is only valid under fairly low dosages of light (first positive phototropism). When further increasing the light dosage, Pringsheim (1909) and Clark (1913) stimulated a weak negative response (first negative phototropism), while even higher amounts of light restored a positive phototropic response (second positive phototropism).

Following the adoption of *Arabidopsis* as a model organism for plant biology research during the 1980s, Poff and associates conducted a series of detailed studies characterizing how light wavelength and dosage affect the first and second positive phototropic responses of etiolated *Arabidopsis* hypocotyls (Steinitz and Poff, 1986; Konjevic et al., 1989; Janoudi and Poff, 1990, 1991, 1992, 1993; Janoudi et al., 1992). These important physiological studies demonstrated that light signaling involved in pulse-induced phototropism is complex, with both additive and opposing effects on the development of hypocotyl curvature (Janoudi and Poff, 1993). Salomon et al. (1997) have proposed that the complex fluence response curve associated with pulse-induced phototropism is related to the localization and magnitude of phototropin phosphorylation. However, this model awaits testing, and more research is needed to understand the underlying basis for the complex fluence curve of pulse-induced phototropism.

CONCLUSIONS

The history of phototropism is long and rich. Our current understanding of the response has its roots in ancient Greek philosophy and stems from the early physiological studies of the enlightenment. Recent research with *Arabidopsis* has tremendously expanded our mechanistic understanding of phototropism. We can no longer view the response as a simple or linear physiological response. Instead, phototropism must be viewed as a complex biological response involving interactions of multiple photoreceptors, multiple hormones, and multiple signaling pathways that together orchestrate the establishment of coordinated differential growth gradients. Given its complexity, much phototropism research remains to be done before we can understand all of the underlying mechanisms and know the full account of its biological significance.

ACKNOWLEDGMENTS

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